Atti Soc. it. Sci. nat. Museo civ. Stor. nat. Milano, 147 (II): 305-315, Giugno 2006

Anna Alessandrello & Giacomo Bracchi

Late Ordovician arachnomorph arthropods from the Anti-Atlas (Morocco)

Abstract – Fossils of the arachnomorph arthropod *Duslia* Jahn, 1893 from the Upper Ktaoua Formation (Caradoc, Late Ordovician) of the Erfoud-Rissani-Alnif-Zagora area (south-eastern Morocco) are herein described. The fossils consist of imprints of approximately 50 dorsal exoskeletons. Previously unknown features of the cephalic shield and the telson-like structure are discussed. Some considerations on the mode of life are proposed.

Key-words: Ordovician, Moroccan Lagerstaetten, enigmatic metazoans.

Riassunto – Artropodi aracnomorfi tardo ordoviciani dell'Anti-Atlante (Marocco).
Vengono descritte alcune decine di impronte di esosheletri dorsali attribuibili all'artropode aracnomorfo *Duslia* Jahn, 1893. Tali impronte sono state rinvenute nelle arenarie tardo ordoviciane (Caradoc) della Formazione Ktaoua Superiore, affioranti nell'area di Erfoud-Rissani-Alnif-Zagora (Marocco sud-orientale). Sono di seguito discussi aspetti precedentemente non noti della morfologia di scudo cefalico e telson unitamente ad alcune considerazioni paleoecologiche.

Parole chiave: Ordoviciano, Lagerstaetten del Marocco, metazoi enigmatici.

Introduction

The aim of this work is to describe approximately 50 specimens of arachnomorph arthropods collected from the Ordovician sandstones of the Erfoud-Rissani-Alnif-Zagora area (Ouguenate-Tafilalt, south-eastern Morocco), a subdesert region of the north-eastern Anti-Atlas.

The study material consists of exoskeletal imprints of cheloniellid arachnomorph arthropods. The fossil record of the Cheloniellida (Dunlop & Selden, 1997; Dunlop, 2002) may include: *Cheloniellon* Broili, 1932 (Devonian, Hunsrück Slate, Germany), *Duslia* Jahn, 1893 (Ordovician, Czech Republic), *Neostrabops* Caster & Macke, 1952 (Ordovician, Ohio), *Paraduslia* Dunlop, 2002 (Devonian, Russia), *Pseudarthron* Selden & White, 1984 (Silurian, Scotland) and *Triopus*

Museo di Storia Naturale, Corso Venezia 55, 20121 Milano, Italy,
e-mail: anna.alessandrello@comune.milano.it; mojak@inwind.it

Barrande, 1872 (Ordovician, Slovakia). In the opinion of Hou & Bergström (1997), only *Chelonellion* should be assigned to the Cheloniellida while *Neostrabops* shows affinities with the Aglaspidida. Furthermore, the same authors recognize the Cheloniellida as a distinct arthropod sister clade to the Chelicerata, although their relationships to the other arachnomorph arthropods remain putative and substantially unresolved.

However, the most recent phylogenetic analyses (Edgecombe & Ramsköld, 1999; Cotton & Braddy, 2004) suggest the existence of two major clades within the Arachnomorpha (= Arachnata): a 'trilobite-allied' clade including trilobites, xandarellids, helmetiids, tegopeltids and naraoiids, and a 'chelicerate-allied' clade including chelicerates, megacheirans, *Emeraldella*, *Sidneyia*, aglaspidids and cheloniellids.

The specimens herein described are assigned to the enigmatic genus *Duslia* Jahn, 1893, which includes only the Caradoc species *Duslia insignis* Jahn, 1893 from the Barrandian area (Czech Republic). Since it was first established *Duslia* has been tentatively assigned to the chitonid molluscs (Jahn, 1893), the polyplacophoran molluscs (Knorre, 1925) and the burlingiid trilobites (Broili, 1933) but it was only in recent times that its arthropod affinities have been definitively recognized (Chlupáč, 1965, 1988).

Study area

Extensive outcrops of Ordovician sandstones and argillites, in places overlain by Quaternary deposits, characterize the Erfoud-Rissani-Alnif-Zagora area (Carte Géologique du Maroc 1/200,000, Todrha-ma'der, 1988). The examined specimens are from a site 16 km east of Rissani, near the boundary between the Ouguenate and Tafilalt regions. The arachnomorph arthropods herein described were collected from the quartzose and coarse-grained sandstones of the Lower Ktaoua Formation (Caradoc, Late Ordovician). In addition to the arachnomorph arthropods some *Cruziana*-like fossil traces and fragmentary agnostoid trilobites are also preserved in these sandstones.

Previous paleontological studies of the Erfoud-Rissani-Alnif-Zagora Ordovician concerned the Arenig (Early Ordovician) sandstones of the Upper Fezouata Formation (Van Roy, 2003; Van Roy *et al.*, 2004) and the Ashgill (Late Ordovician) sandstones of the Upper Ktaoua Formation (Samuelsson *et al.*, 2001; Van Roy, 2001, 2004; Alessandrello & Bracchi, 2003). Arthropod fragments of aglaspidid and eurypterid affinity, a single complete specimen of a possible basal chelicerate and several hundred specimens of the discoidal organisms *Eldonia* and *Protolyella* have been recognized from the Ashgill strata. The Arenig sandstones have yielded echinoderms, sponges such as *Choia*, *Pirania* and *Hamptonia*, vermiform organisms including annelids and a possible planarian, a tuboid graptolite, a *Tremaglaspis*-like aglaspidid arthropod, large bivalved arthropod carapaces, trilobites and a plumulitid machaeridian. The presence of cheloniellid arachnomorph arthropods belonging to *Duslia* in the Ordovician sandstones of the Erfoud-Rissani-Alnif-Zagora area has been reported both for the Ashgill (Van Roy, 2001: 50 specimens from 3 sites) and Arenig sandstones (Van Roy, 2003, pg. 51: unspecified number of specimens of <<[...] a new cheloniellid.>> from a single site) but a detailed description of these specimens has not been published to date.

Material and methods

Forty-seven specimens of *Duslia* from a site near Rissani are examined in the present study. The specimens are held in the paleontological collections of the Museo Civico di Storia Naturale di Milano and they are labelled with the abbreviation 'MSNM' followed by the series number of the invertebrate collection (i).

The fossils of *Duslia* from the Rissani area consist of dorso-ventral imprints of the dorsal exoskeleton in a brownish, greenish, greyish or reddish sandstone. It was not possible to distinguish the dorsal and the ventral surfaces of the exoskeleton in any of the studied specimens. The specimens are preserved as external molds (negative hyporelief) or counterpart casts (positive epirelief). In two cases (MSNM i25272, MSNM i26796) both the hyporelief and epirelief of 2 specimens are preserved. In 13 specimens (MSNM i25272#1, MSNM i25272#2, MSNM i25277, MSNM i25279, MSNM i25280, MSNM i25281, MSNM i25292, MSNM i25297, MSNM i25304, MSNM i25310, MSNM i25313, MSNM i25315 and MSNM i25317) both the external mold and the counterpart cast are preserved. The complete imprint of the exoskeleton is preserved in 10 specimens (MSNM i22782, MSNM i22787, MSNM i22790, MSNM i22792, MSNM i25272#1, MSNM i25288, MSNM i25292, MSNM i25304, MSNM i25309 and MSNM i25316).

The systematic paleontology section below follows the scheme by Hou & Bergström (1997): the arachnomorph arthropods have been included here within the Superclass Lamellipedia Hou & Bergström, 1997 which corresponds to the Subphylum Arachnomorpha Heider, 1913 emend. Størmer, 1944 (as phylum) and to the Subphylum Trilobitomorpha Størmer, 1944.

Systematic Paleontology

Phylum Schizoramia Bergström, 1976
Superclass Lamellipedia Hou & Bergström, 1997
Class Artiopoda Hou & Bergström, 1997
Subclass Petalopleura Hou & Bergström, 1997
Order Cheloniellida Broili, 1933
Family Cheloniellidae Broili, 1933
Genus *Duslia* Jahn, 1893
Duslia cf. *D. insignis* Jahn, 1893

Material: 47 specimens. MSNM i22781, MSNM i22782, MSNM i22783, MSNM i22785, MSNM i22786, MSNM i22787, MSNM i22788, MSNM i22789, MSNM i22790, MSNM i22791, MSNM i22792, MSNM i22793, MSNM i22794, MSNM i22797, MSNM i22799, MSNM i22827, MSNM i25272#1, MSNM i25272#2, MSNM i25277, MSNM i25279, MSNM i25280, MSNM i25281, MSNM i25282, MSNM i25283, MSNM i25286, MSNM i25287, MSNM i25288, MSNM i25289, MSNM i25291, MSNM i25292, MSNM i25293, MSNM i25295, MSNM i25297, MSNM i25300, MSNM i25301, MSNM i25303, MSNM i25304, MSNM i25306, MSNM i25309, MSNM i25310, MSNM i25311, MSNM i25313, MSNM i25315, MSNM i25316, MSNM i25317, MSNM i26796#1 and MSNM i26796#2.

Locality: Rissani, Tafilalt, Morocco.

Geological age: Caradoc (Late Ordovician).

Measurements: values for maximum length and width have been measured only on complete specimens. The maximum width-maximum length ratio ranges from 0.63 (MSNM i22790: 102 mm L, 65 mm W; MSNM i25292: 102 mm L, 65 mm W) to 0.71 (MSNM i22782: 99 mm L, 71 mm W; MSNM i25309: 71 mm L, 51 mm W).

Description: the exoskeleton imprint indicates a broadly oval and clearly trilobate body shape. The cephalon (cephalic shield), thorax and telson as well as two symmetrical pleural lobes and an axial lobe (rhachis) may be distinguished.

The trilobite-like cephalon has an overall semicircular outline and a smooth, flattened surface. In some specimens (MSNM i22785, MSNM i22799, MSNM i22827) the genal region is marked by short branches of narrow and shallow furrows that seem to radiate from the glabellar area suggesting that it is differentiated into sub-regions. However, the complete development of furrows and sub-regions was not observed in any specimen. Two sub-circular, symmetric and gently concave depressions on both sides of the glabella are evident in the genal region of two specimens (MSNM i22790, MSNM i25272#1) and may represent traces of the ocular areas. The fusiform glabella does not extend as far as the anterior margin of the cephalon and it is separated from the genal region and pre-glabellar field by a deep furrow. Other furrows (2-3 in number) produce a transversal lobation of the glabella. In most of the studied specimens, the posterior margin of the cephalic shield is marked by a shallow and narrow depression that separates the entire cephalon from the thorax. In some specimens (MSNM i22790, MSNM i22827, MSNM i25792) some short, subcylindrical spines of equal length (1-2 mm) are preserved on the outer margin of the cephalon. Imprints of single spines or groups of spines appear in various positions along the entire outer margin of the cephalic shield but these do not seem to form a continuous series in any of the specimens. Due to the coarse-grained nature of the sediment enclosing the fossils the ultrastructure of these tiny spines is not preserved.

The thorax appears to consist of ten broad, gently convex, radially arranged and smooth tergites. The boundaries between adjacent pleurae are marked by rather broad, concave furrows that radiate from the axial lobe in a similar manner to the pleurae. The furrows may represent traces of the intertergite boundaries. The first pleura is antero-laterally directed while the last one is postero-laterally directed. The change in direction takes place between the second and the third pleura. The width of the pleurae seems to decrease slightly towards the pygidium, but it was not possible to establish whether this character is a result of the overlapping of adjacent tergites which thus may obscure the true width of the pleurae. A gradual reduction of the length of the pleurae from the anterior to the posterior margin of the body is evident. All the pleurae widen slightly abaxially. It was noted in 12 specimens only that the abaxial margin of some left and right pleurae bear a few isolated spines identical to those described for the outer margin of the cephalon. The rhachis is made up of 10 convex rings (somites) of almost equal length and width with the exception of the most posterior rings that tend to assume a fusiform shape. The most posterior ring becomes slightly pointed at the posterior end, where a telson is inserted. Adjacent rings are separated by wide, deep furrows which are in turn connected with the furrow that marks the boundary of the entire axial lobe.

Fig. 1 - *Duslia* cf. *insignis*, MSNM i25272a#1 (x 0.6).

The telson is very poorly preserved and evident in just a few specimens (MSNM i22781, MSNM i22797, MSNM i25272#1, MSNM i25315, MSNM i25316), probably due both to its tiny dimensions and to the coarse-grained matrix that encloses the fossils. However, in MSNM i22781, MSNM i22797, MSNM i25315 and MSNM i25316 it may be seen to be clearly formed of only 2 narrow and elongate furcae. Between the paired furcae of MSNM i25272#1 the imprint of a small subtrapezoidal structure is preserved. This structure has a rounded posterior margin so that it appears to be fan-shaped. Unfortunately, the structural comparison of the elements of the telson and between the telson and the axial lobe is a little bit confusing due to poor preservation. No spines are evident along the telson margin in any of the specimens studied.

Discussion

The exoskeleton of the specimens studied exhibits a strong similarity to that of trilobites as it is both longitudinally and transversally trilobed. However, the absence of a pygidium and the presence of a telson-like structure clearly indicates that *Duslia* is not a trilobite but a trilobite-like arachnomorph arthropod. Moreover, like the cheloniellid arachnomorph arthropods (Dunlop, 2002), the fossils described in this work possess a broadly oval shape, a series of pleurae radiating from a narrow axial region deeply penetrating onto the cephalic shield, and a furcate structure at the posterior margin. This type of organization may in particular be compared with that of the monospecific cheloniellid genera *Duslia* and *Paraduslia*. However, *Paraduslia talimaae* Dunlop, 2002 possesses at least 12 tergites (Dunlop, 2002), while in *Duslia insignis* (Chlupáč, 1988) and in the specimens studied here only 10 tergites are present. Furthermore, in *Paraduslia talimaae* the shape of the anterior margin of the rhachis is different to that of the Czech and Moroccan specimens of *Duslia*, being not perfectly fusiform but forming a raised diamond-shaped area (Dunlop, 2002).

The dorsal exoskeleton is the only part of the body structure which is evident as imprints in the Moroccan specimens of *Duslia*. This kind of preservation suggests that the exoskeleton of *Duslia* was to a lesser or greater degree sclerotized. The specimens from the Rissani area show only the ventral or the dorsal surface of the dorsal exoskeleton even if a distinction between the two surfaces has never been possible.

The first morphological difference to be noted between the specimens described from Czechoslovakia (Chlupáč, 1988) and Russia (Dunlop, 2002) and those described in the present study regards the spines of the margin of the exoskeleton. These spines appear to be absent in the only 4 specimens known of *Paraduslia talimaae* while in *Duslia insignis* they clearly form a continuous fringe. In the Moroccan specimens, a few isolated or grouped spines have been observed only along the cephalon and the margin of the tergites, but this difference can not be assumed as crucial to identify a new species. It is reasonable to hypothesize the presence of a continuous series of spines along the exoskeleton outline of both *Paraduslia talimaae* and the specimens from the Rissani area given the poor preservation. The preservation of these spines as imprints probably suggests, in a similar manner to the exoskeleton, that they were sclerotized expansions of the dorsal shield.

Fig. 2 - *Duslia* cf. *insignis*, MSNM i22785 (x 0.7).

Fig. 3 - *Duslia* cf. *insignis*, MSNM i 22781 (x 0.8).

Fig. 4 - *Duslia* cf. *insignis*, MSNM i 22827 (x 0.5).

The telson of both *Duslia insignis* and *Paraduslia talimaae* seems to lack the fan-shaped structure of the Moroccan specimens. However, the presence of a small rounded telson associated with a pair of furcae has been observed by Van Roy (2003) in *Duslia* specimens from the Lower Ordovician of the Zagora area (south-eastern Morocco).

Moreover, both *Duslia insignis* and *Paraduslia talimaae* appear to lack eyes (Chlupáč, 1988; Dunlop, 2002). However, the genal region of specimens MSNM i22790 and MSNM i25272#1 from the Rissani area seems to preserve traces of two concave ocular areas on both sides of the glabella. Even if the presence of eyes in *Duslia* remains equivocal, their eventual presence may be in agreement with the diagnosis of the arachnomorph arthropods proposed by Hou & Bergstrom (1997, pg. 42: <<[...] eyes are originally ventral, but there is a strong tendency to shift them to the dorsal side of the head [...]>>). In addition, the shape of the ocular areas of the specimens from the Rissani area and the type of preservation, which includes only an imprint of the exoskeleton, seem to suggest that the eyes of *Duslia* were dorsal in position. In the opinion of Chlupáč (1988) and Dunlop (2002), the lack of eyes in *Duslia* and *Paraduslia* suggests a burrowing mode of life for these organisms either on or just within the substrate. However, if *Duslia* really possesses dorsal eyes as the Moroccan specimens seem to indicate, an epibenthic mode of life seems more likely.

Acknowledgements

Authors wish to thank the Service Geologique du Maroc for the useful cooperation and Giorgio Teruzzi for the precious advices.

Photographic material thanks to Roberto Appiani.

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Ricevuto: aprile 2006
Approvato: maggio 2006